THE STRUCTURE AND DEVELOPMENT OF THE BARK IN THE SASSAFRAS.

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(WITH NINE FIGURES)

THE common sassafras occupies a somewhat isolated position among northern trees. It is not only the single living representative of the genus Sassafras, but it belongs to the Lauraceae, a family with many arboreal genera in tropical and subtropical regions, but with very few in the cooler parts of the earth. The tree is further remarkable because its young branches remain green for a considerable period, differing in this respect from the majority of the trees among which it grows. For these various reasons it was hoped that a study of the bark might reveal features of interest.

MÖLLER has already studied the bark in several genera of the Lauraceae and has included in his published account a short description of what he found in the sassafras.[1] According to his researches the family as a whole is characterized by the following peculiarities in the bark: a late appearance of cork; an epidermal origin of the phellogen; a slight development of collenchyma in the outer cortex, most of the cells remaining thin-walled and parenchymatous; the occurrence of stone-cells in the medullary rays between the strands of primary sclerenchyma; the presence of ethereal oil and slime in some of the parenchyma cells; the scattered bast fibers in the inner or secondary bark. With regard to the sassafras in particular he notes that the cork is homogeneous and composed of thin-walled cells and that the inner bark is destitute of stone cells. It should be remarked that most of MÖLLER'S material in this family consisted of dried bark, much of which was fragmentary and in poor condition.

In his more general account of the Lauraceae SOLEREDER accepts the majority of MÖLLER'S statements with regard to the bark.[2] Quoting from J. E. WEISS, however, he notes the fact that the phellogen is not invariably epidermal in origin, but that it is sometimes derived

[1] Anat. der Baumrinden 103–110. 1882.

[2] Syst. Anat. der Dicot. 795. 1899.

from the layer of parenchyma just within the epidermis. He also remarks that the secondary bast fibers, although usually scattered, form distinct strands in certain genera, and that the individual fibers are normally four-sided in cross section with narrow lumina.

The present investigation is based on material collected near New Haven, Connecticut, and is confined to the stem and its branches, no reference being made to the bark of the root. The tissues described may be classified as follows:

PRIMARY TISSUES	SECONDARY TISSUES
Epidermis	Tissues derived from the cambium ring
Outer cortex	The phellogen and its derivatives
Primary medullary rays	
Primary bast	

PRIMARY TISSUES.

Epidermis.

The epidermal cells are characterized by a strongly thickened cuticle. Close to the growing point they are isodiametric and thin-walled, but the cuticle begins to make its appearance very early and

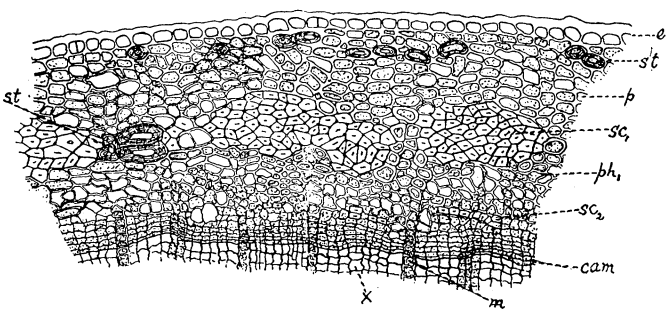


FIG. 1.—Cross-section through bark one year old. ×70. *cam*, cambium ring; *e*, epidermis; *m*, medullary ray; *p*, parenchyma; ph_1, primary phloem; sc_1, primary sclerenchyma; sc_2, secondary sclerenchyma; *st*, stone cells; *x*, xylem.

practically completes its development during the first year's growth. At the close of this period it occupies about half the thickness of the epidermis (*fig. 1*). During the elongation of the stem the epidermal cells retain the power of growth and division. Since their growth is largely in a longitudinal direction, the cell-division is mainly brought about by transverse walls, division by longitudinal walls being much

more infrequent. In an epidermis a year old, seen from the surface, the boundaries of the original epidermal cells can usually be distinguished. They are somewhat thicker than the secondary transverse walls, which in turn are thicker than the secondary longitudinal walls (*fig. 2*). With the formation of cork the epidermis is of course split longitudinally and soon begins to undergo disorganization. No trace of it is left in a tree 8^{cm} in diameter.

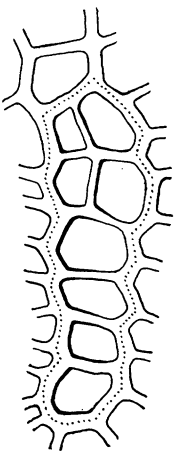


FIG. 2.—Surface view of epidermal cells. ×320. The dotted line represents the boundary of the original cell, which has undergone division.

The number of stomata produced varies greatly, but seems to be largely dependent upon external conditions. A rapidly growing tree, for example, in a moist locality has many stomata, while a slow-growing tree in dry soil develops very few. The stomata are depressed and the epidermal cells bounding the guard cells are somewhat modified, being longer and narrower than their neighbors (*fig. 3*). Most of the stomata are transverse to the axis upon which they are borne, a few are oblique, but apparently none of them occupy a longitudinal position. This is doubtless to be explained by the fact that the stomata are formed late in the development of the epidermis, the wall separating the guard cells representing one of the secondary transverse divisions of an epidermal cell. In the majority of cases the cells surrounding a stoma contain anthocyan, so that to the naked eye the stomatal region looks like a minute red speck in the epidermis. This peculiarity affords a ready means for detecting the stomata.

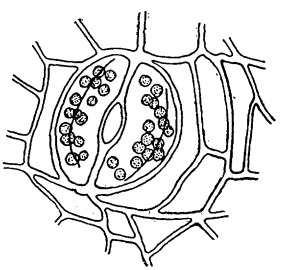


FIG. 3.—Stoma with surrounding cells, surface view. ×320.

Epidermal hairs are developed on very young twigs before the primary tissues are fully differentiated. They are simple and unicellular, with thickened walls, and scarcely extend below the cuticle (*fig. 4*). These hairs never persist through the first vegetative period, but dry up and fall away as soon as the cuticle begins to thicken. Their former position is often marked by

small concave depressions in the cuticle. The number of the hairs varies, and in a general way is inversely proportional to the number of stomata. Thus, in a moist locality few hairs are formed, while in a dry region they are very abundant. In a mesophytic area some trees bear few hairs, while others under the same conditions bear very many. It would appear from this that the production of hairs was primarily due to individual peculiarities of the tree in question and secondarily to the external conditions under which the tree developed.

FIG. 4.—Epidermal hairs on a twig one month old. ×50.

Outer cortex.

The outer cortex comprises everything external to the primary sclerenchyma except the epidermis. It is composed of a ground mass of parenchyma with scattered stone-cells. No crystal cells occur. With the formation of cork the outer cortex gradually becomes disorganized and eventually disappears.

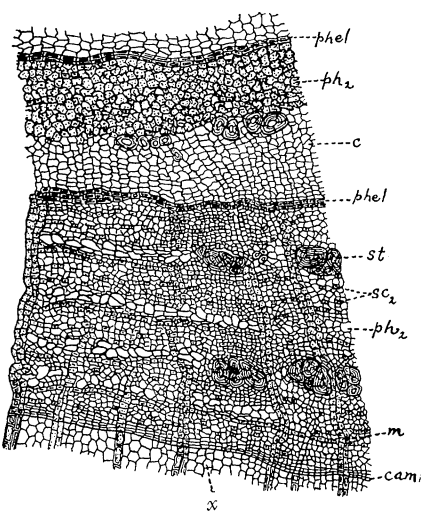
In cross section the parenchyma cells vary from elliptical to rectangular in outline, the long diameter running in a tangential direction (*fig.* 1, *p*). They vary considerably in size and some of the larger cells have their walls slightly lignified. Most of the cells, however, have thin walls, which may or may not be provided with simple pits. Many of the smaller cells contain starch and this is especially likely to be true of those which border the strands of sclerenchyma. The presence of ethereal oil in the parenchyma can be demonstrated by appropriate tests, but it does not seem to be localized in special cells. In all probability the oil represents an excretory product of the protoplasm of the parenchyma cells, and this fact would account for its general distribution.

The stone cells form a continuous or interrupted layer extending entirely around the stem (*fig.* 1, *st*). They sometimes lie next to the epidermis and are sometimes separated from it by one or two layers of parenchyma cells. The stone cells are at first circular in cross section but afterwards become flattened and assume an elliptical outline. In radial section they appear rectangular, being about three times as long as broad. Their walls are strongly thickened by deposits of

ligno-cellulose in distinct layers, and these are pierced by numerous simple and branched pits.

Primary medullary rays.

The primary medullary rays extend from the cambium to the outer cortex, the ray cells merging into the cortical cells without a distinct line of demarcation. The outer portion of the ray is of course directly differentiated from the meristem at the growing point, while the inner portions owe their existence to the activity of the cambium. Some of the cells in the outer portion retain their power of growth and division for several years, the majority of the dividing



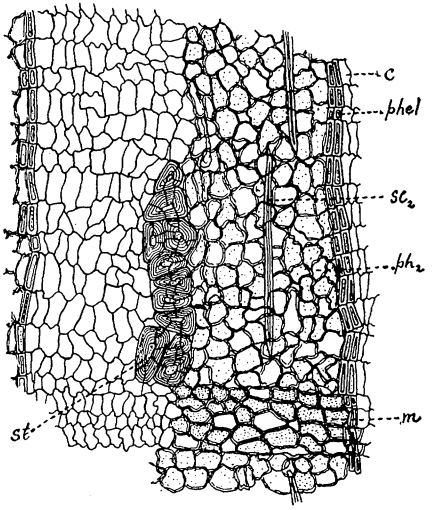


FIG. 5.—Cross section through old bast. ×25. FIG. 6.—Radial section through old bast. ×75. *c*, cork; *cam*, cambium ring; *e*, epidermis; *m*, medullary ray, *p*, parenchyma; ph_2, secondary phloem; *phel*, phelloderm; sc_2, secondary sclerenchyma; *st*, stone cells; *x*, xyiem.

walls being radial. Thus, in a stem one year old, the strands of primary sclerenchyma are separated by from two to five layers of cells, in a stem two years old by as many as fifteen layers, while in a stem four years old the number may be increased to thirty or more. Since the portions of the rays derived from the cambium do not undergo further divisions, they remain permanently from one to three cells in width. In consequence of these facts the rays gradually assume a T-shape

in cross section. This form is retained until the outer cortex has become disorganized, after which they appear like narrow bands (*fig. 5, m*). In radial section the rays are from four to fourteen cells across (*fig. 6, m*).

In most of the ray cells the walls are slightly thickened and provided with numerous simple pits. They usually contain starch and sometimes ethereal oil as well. When the cells are cut off by cork the starch disappears, showing that it is completely utilized; the oil, on the other hand, persists. Some of the ray cells between the strands of primary sclerenchyma become strongly sclerotic, and in some cases cells of this character completely bridge the space from one strand to another (*fig. 1*). They can be easily distinguished from the sclerenchyma cells, even in cross section, by their larger size and distinct lamination. In longitudinal section they appear short and resemble the stone cells of the outer cortex.

Primary bast.

The primary sclerenchyma occurs in well-defined bundles, averaging about fifty fibers apiece (*figs. 1, 8, sc_1*). Most of these bundles, in a radial direction, measure from three to eight cells across. In most of the fibers the wall is so strongly thickened that the cavity is reduced to a mere slit; in some cases, however, the thickening is less and this is especially likely to be true in the middle of a bundle. Apparently the deposition of ligno-cellulose upon the cell walls is not completed until the second vegetative period.

The primary phloem lies just within the primary sclerenchyma, between the latter and the secondary sclerenchyma, and forms a band from three to five cells across in a radial direction (*fig. 1, ph_1*). The sieve tubes are more or less completely separated from the sclerenchyma by a layer of phloem parenchyma. The cells of this layer tend to be rectangular in cross section, and their slightly thickened walls have numerous simple pits. The sieve plates separating the segments of the sieve tubes are nearly always somewhat oblique; they are supplemented by numerous lateral sieve plates, especially in the radial walls of the tubes. All of the sieve plates in the primary phloem soon become covered by deposits of callus. The companion cells conform to the usual type.

SECONDARY TISSUES.

Tissues derived from the cambium ring.

The tissues of the bark, regularly derived from the cambium ring, include the secondary sclerenchyma and the secondary phloem. In addition to these, scattered groups of stone cells, which should probably be considered a part of the phloem, also make their appearance. Of course the cambium also adds new elements to the primary medullary rays and brings about the development of the secondary rays (*figs. 1, 5*). The development of these various secondary tissues begins during the first vegetative period.

The fibers of the secondary bast do not form bundles. Some of them form interrupted layers arranged concentrically in the stem, others are scattered through the secondary phloem. The layers are usually but a single cell across and are separated from one another by several layers of phloem. The individual fibers are rectangular in cross section and about thirty times as long as broad; their walls are very strongly thickened (*figs. 1, 5, 6, sc_2*). When the bast fibers are cut off by cork all regularity in their arrangement disappears.

The sieve tubes of the secondary phloem, except those earliest formed, are arranged in interrupted, concentric layers, one or two cells across (*fig. 5, ph_2*). Many of the sieve tubes are in direct contact with the medullary rays, but very few of them adjoin the sclerenchyma fibers. The tubes exhibit essentially the same structure as those in the primary phloem. On account of their delicate walls they become practically indistinguishable when cut off by cork.

The bulk of the secondary phloem is composed of parenchyma. When first differentiated from the cambium the cells of this tissue are closely packed together, rectangular in outline, and destitute of intercellular spaces. As they become pushed outward, their outlines become more rounded and minute intercellular spaces appear. Their walls are fairly thin but are provided with simple pits. Until they are cut off by cork the parenchyma cells are arranged in layers, which lie among the layers of sclerenchyma and sieve tubes.

The groups of stone cells are irregularly scattered in the secondary bast but always abut against a medullary ray (*fig. 5, st*). Such a group in cross section is often larger than a bundle of primary sclerenchyma and is composed of larger elements. The stone cells are the

most conspicuous structures found in the inner bark, and are even more striking in appearance than those found in the outer cortex. In longitudinal section (*fig. 6, st*) they show the same outlines as in cross section (*fig. 7*) and are therefore isodiametric. Their strongly thickened walls show a very distinct lamination and their contracted cavities are connected by numerous simple and branched pits. Probably on account of poor material, these stone cells were not seen by MÖLLER.

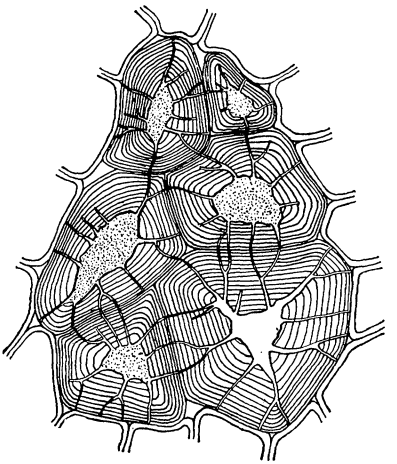


FIG. 7.—Stone cells from inner bark, cross section. ×450.

The phellogen and its derivatives.

The derivatives of the phellogen are the lenticels, the cork, and the phelloderm. The lenticel phellogen is the first to make its appearance; the primary cork phellogen is, at least in part, a direct extension of the lenticel phellogen; and the succeeding phellogens arise more or less independently from the deeper layers of the bark. The primary cork phellogen first appears on the south side of an erect stem and normally on the upper surface of a horizontal branch. From these regions it gradually extends laterally and usually forms a complete layer in the course of three or four years. The development, however, follows no definite rule. For example, in one eight-year old stem there was no cork on the north side except in the immediate vicinity of the lenticels, while in another stem of the same age there were five layers of cork on the south side and three on the north. These observations show that a phellogen layer may be active in one part although it has ceased to be functional in another. They also show that there is no definite relationship between the age of the stem or branch and the number of layers of phellogen. The early appearance of cork in the regions exposed to the sun is probably due to the fact that the sassafras is an intolerant species and that the cork protects the deeper tissues from sun scalding.

The primary lenticels are always formed directly beneath the stomata, following in this respect the general rule first enunciated by TRECUL.[3] Some of the lenticels never break through the epidermis but remain in an undeveloped condition. The lenticel phellogen arises from the layer of cells just within the epidermis. The thin-walled complementary cells are at first closely packed together. After about twelve layers of these cells are formed the epidermis is ruptured, and the complementary cells as they become exposed separate from each other and present very irregular and distorted outlines. The mature lenticel agrees with the second of the types described by DEVAUX[4] and shows no distinct layers of cork among the comple-

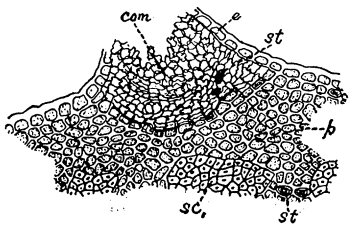


FIG. 8.

plementary cells (*fig. 8*). In some cases, however, a lenticel contains a few scattered stone cells (*fig. 8, st*). Secondary lenticels are developed from secondary phellogens and make their appearance in the splits of the bark. These lenticels break through the

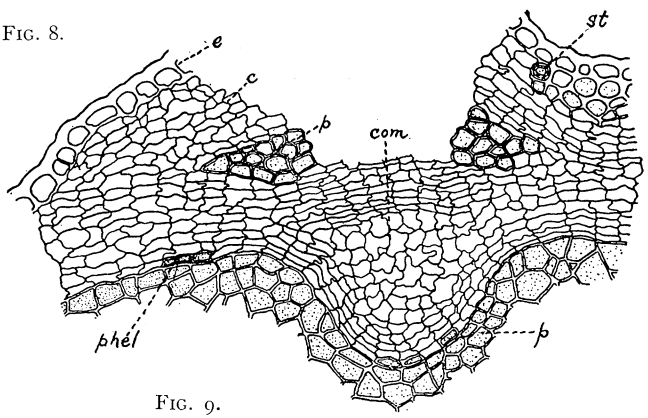


FIG. 9.

FIG. 8.—Section through a primary lenticel. ×55. FIG. 9.—Section through a secondary lenticel. ×60. *c*, cork; *com*, complementary cells; *e*, epidermis; *p*, parenchyma; *phel*, phelloderm; sc_1, primary sclerenchyma; *st*, stone cells.

layers of cork and parenchyma cells which enclose them and eventually exhibit the same structure as the primary lenticels (*fig. 9*).

Since the primary cork phellogen is a direct extension of the lenticel phellogen, it is never epidermal in origin but is always derived

[3] Compt. Rend. **73**:15. 1871. [4] Ann. Sci. Nat. Bot. VIII. **12**:61. 1900.

from the subepidermal parenchyma. In the majority of cases it arises from the layer of cells just inside the epidermis. Sometimes, however, it is derived from the second, third, or fourth layer, and this is always the case when stone cells are present next the epidermis. It thus frequently happens that the different parts of the phellogen do not all arise from the same layer of cells. The secondary layers of phellogen are largely derived from the parenchyma cells in the secondary phloem. When stone cells are present in the parenchyma the phellogen often bounds them on the inside. The phellogen forms concentric layers in the stem, but these layers are not altogether independent. In certain regions two layers will coalesce, in other regions they will be separated from each other by several layers of cells. Even the outermost of the secondary phellogens is more or less united with the primary phellogen.

The cork, as already noted by MÖLLER, is of the ordinary type. It consists of empty cells arranged in radial rows, and the walls are thin and suberised (*figs. 5, 6, 9, c*). In most cases from ten to twelve layers are formed by each phellogen. The structure of the cork is not uniform throughout the Lauraceae; in certain genera it consists of two kinds of cells arranged in more or less definite layers; namely, thin-walled cells and cells in which the inner tangential walls are thickened.[5]

The phelloderm in the sassafras forms a most characteristic feature of the bark. When derived from secondary phellogens it consists almost entirely of strongly flattened cells with thick lignified walls, provided with simple and branched pits. The flattening is in a radial direction, and the cells show the same rectangular outlines in both radial and transverse sections (*figs. 5, 6, phel*). The phelloderm is arranged in layers from one to three cells thick. The layer derived from the primary phellogen differs from the others in being composed of both thin-walled and thick-walled cells. In the case of lenticels the thick-walled phelloderm cells are few and scattered and are sometimes absent altogether. Lignified phelloderm does not seem to be of very frequent occurrence. According to J. E. WEISS[6] it is to be found in species of Cytisus and Philadelphus; KUHLA[7]

[5] See MÖLLER, Anat. der Baumrinden 103. 1882.

[6] Beiträge zur Kenntniss der Korkbildung. Denkschr. Königl. Bayer. Bot. Gesells. **6**: 61. 1890.

[7] Bot. Centralbl. **71**: 196. 1897.

describes it for *Ptelea trifoliata*, and SOLEREDER[8] notes its appearance in several genera of the Saxifragaceae other than Philadelphus. It therefore occurs in widely scattered families and probably has but little taxonomic significance.

SUMMARY.

Among the more interesting points brought out by this study are the following: the early thickening of the cuticle; the variation in the number of epidermal hairs and stomata; the early formation of cork in regions exposed to the sun; the stone cells in the outer bark, between the strands of primary sclerenchyma, and in the inner bark; the regular layers of thick-walled phelloderm derived from the secondary phellogens.

The writer is indebted to Professor ALEXANDER W. EVANS for criticism and advice.

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[8] Syst. Anat. der Dicot. 360. 1899.